



The fallacy of a “task-negative” network

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In a neuroimaging study of goal-directed cognition, brain activity will be significantly greater than baseline in a frontoparietal “task-positive” network (TPN). Further, a number of regions will be deactivated in the cinguloparietal “task-negative” network (TNN), or default network. Although this generic statement characterizes many findings in cognitive neuroscience, these network labels are imprecise at best, and also transmit a profound misconception about the functional role of the default network in cognition. The dichotomization of “task-positive” and “task-negative” functional networks perpetuates the notion that the default network is not engaged in active cognitive processes. On the contrary, recent studies challenge this circumscribed view, demonstrating that: (1) the TPN comprises at least two functionally and anatomically distinct networks that play very different roles in cognition; and (2) the TNN (i.e., the default network) is not “task-negative” *per se*, but rather, is often engaged during goal-directed cognition, depending on the nature of the task. Further, (3) recent work demonstrates that components of these networks flexibly interact with one another based on task demands. These interactions raise important questions with respect to the role of the default network in goal-directed cognition and challenge the veracity and utility of a “TPN vs. TNN” distinction.

Engagement of the putative TPN is typically driven by tasks that confound demands for cognitive control and externally directed attention to visually presented stimuli. However, these processes, and their underlying functional neuroanatomy, can be dissociated. Cognitive control operations will engage an extended “frontoparietal control network,” consisting of lateral prefrontal cortex (LPFC), precuneus, the anterior inferior parietal lobule, dorsal anterior cingulate cortex (dACC), and anterior insula (Vincent et al., 2008; Niendam et al., in press; Figure 1A, green regions). Visual attention will engage the “dorsal attention network,” consisting of the

frontal eye fields (FEF), inferior precentral sulcus, middle temporal motion complex (MT+), and superior parietal lobule (SPL; Figure 1A, red regions). While the constellation of regions across the frontoparietal control and dorsal attention networks (i.e., the TPN) may be co-active and coupled during task performance (cf. Badre et al., 2010; Grady et al., 2010; Gordon et al., in press), they need not be under all circumstances.

The default network was first identified by task-induced deactivations, or brain activity associated with a passive fixation “baseline” condition relative to specific attention-demanding visual tasks (Shulman et al., 1997; Raichle et al., 2001). Passive conditions, such as fixation, reliably engage the default network (Toro et al., 2008; Laird et al., 2009), which includes medial prefrontal cortex (MPFC), posterior cingulate cortex (PCC), superior and inferior frontal gyri, medial and lateral temporal lobes, and posterior inferior parietal lobule (pIPL; Buckner et al., 2008; Figure 1A, blue regions).

The terms “TPN” and “TNN” were first introduced by Fox et al. (2005). In this resting-state functional connectivity MRI study, spontaneous low-frequency BOLD signal fluctuations across the brain revealed an anti-phase, or “anti-correlated” relationship between two distinct and dissociable functional-anatomic networks (Fox et al., 2005)¹. Their approach examined whole-brain correlations with *a priori* seed regions. TNN seeds were derived from an earlier meta-analysis of decreases in activity during tasks (i.e., relative to fixation;

Shulman et al., 1997) in MPFC, PCC, and pIPL; TPN seeds were derived from a study of cued attention and working memory and included IPS, FEF, and MT+, all within the dorsal attention network. The alignment of the TPN with the dorsal attention network persisted through the authors’ initial papers (see Fox et al., 2005; Fox et al., 2006). Further, the default network was recognized by Fox et al. (2005) for its role in cognition, as evidenced in part by citing a mental inference study (Gusnard et al., 2001). Since the seminal observations of Fox et al. (2005), the TPN and TNN nomenclature has been widely adopted – likely due to its utility in explaining the persistence of dorsal attention network engagement and default network suppression across many tasks (Toro et al., 2008). However, the functional definition of the TPN, as described above, has expanded to encompass a broad spectrum of goal-directed attention tasks, encapsulating not only the dorsal attention network, but the frontoparietal control network as well² (e.g., Grady et al., 2010; Hampson, 2010; Gordon et al., in press). In contrast, labeling the default network as “task-negative” has fortified its functional status as either deactivated by, uninvolved in, or even antithetical to, goal-directed cognition³ (see Sonuga-Barke and Castellanos, 2007). Unfortunately, characterization of the default network as “task-negative” has inhibited scientific awareness of its critical functional role in active task conditions.

Conceptualization of the default network as a TNN began with the use of fixation as a passive baseline. As a base-

¹The interpretability of negative correlations with the methodological use of mean signal regression has been questioned, as this approach introduces negative correlations between regions (Murphy et al., 2009). However, other observations without using mean signal regression demonstrate the same essential findings (Hampson et al., 2010; Chai et al., 2012).

²Drawing upon the work of Fox et al. (2005), the inclusion of elements of cognitive control to describe the TPN is exemplified by Hampson (2010). “Adopting the terminology of Fox et al. (2005), we refer to these cognitive control regions as ‘task-positive’ areas” (Hampson, 2010, p. 37).

³Also drawing upon the work of Fox et al. (2005), a literal interpretation of a TNN is applied by Sonuga-Barke and Castellanos (2007). “One such network, termed the ‘default-mode’ network is particularly observable during resting-states, and its activation is conjectured to be incompatible with goal-directed activity (Fox et al., 2005)” (Sonuga-Barke and Castellanos, 2007, p. 978).

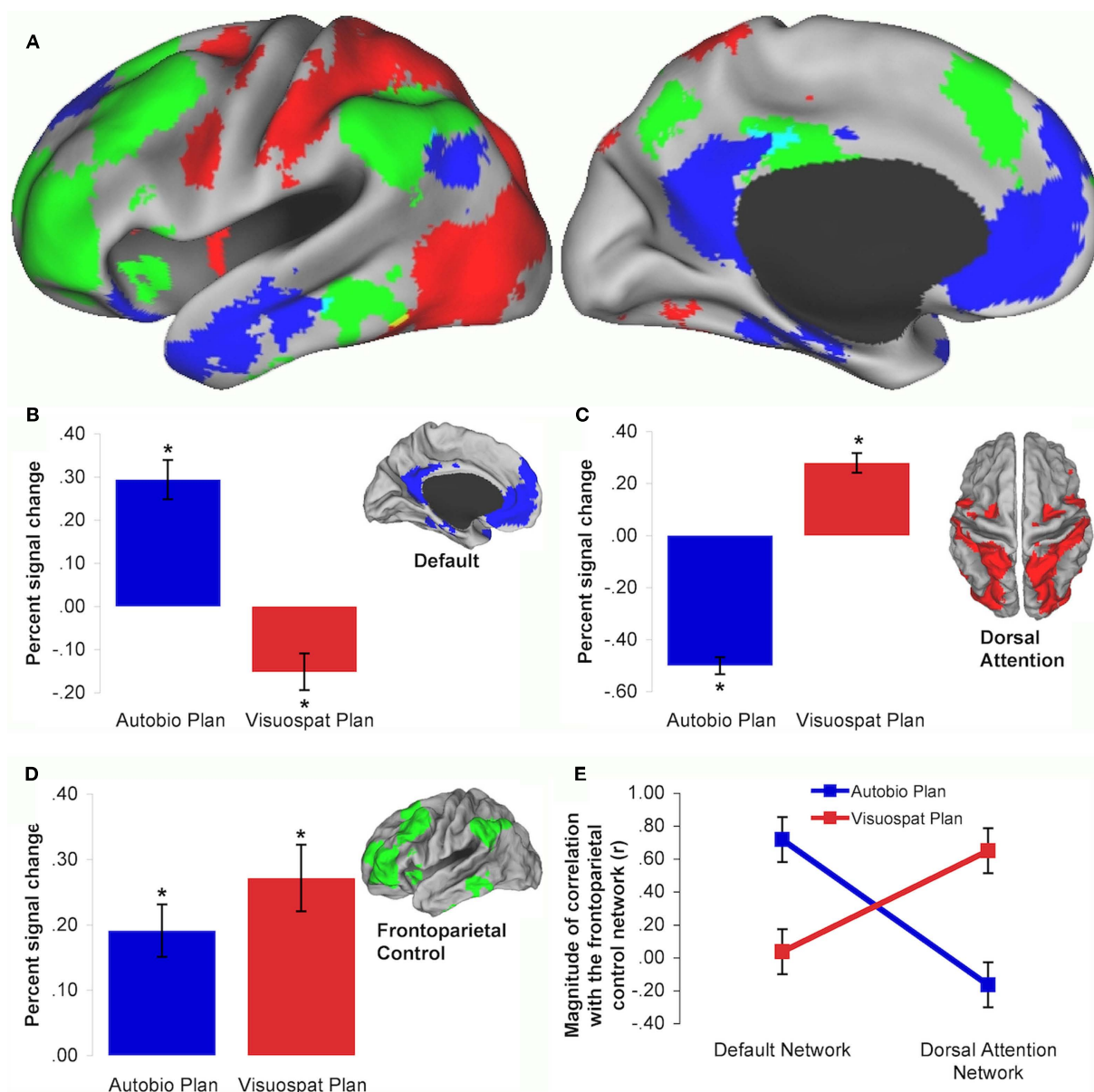


FIGURE 1 | (A) Intrinsic connectivity maps depicting the default (blue), dorsal attention (red), and frontoparietal control (green) networks of the brain. Mean and SEM of planning task-related percent BOLD signal change within each intrinsic connectivity network: **(B)** default network, **(C)** dorsal attention network, **(D)** frontoparietal control network. * indicates significant task difference in BOLD signal from baseline. **(E)** Frontoparietal control network coupling is

modulated by autobiographical and visuospatial planning tasks. Frontoparietal control network activity is coupled with the default network, and decoupled from the dorsal attention network, during autobiographical planning. Frontoparietal control network activity is coupled with the dorsal attention network, and decoupled from the default network, during visuospatial planning. Data are reproduced from Spreng et al. (2010).

line where no overt task is performed, fixation is a reliable method to localize the default network relative to active, externally directed, tasks. Far from being passive however, default activity during fixation is hypothesized to reflect unconstrained and internally focused cognitive processes (Buckner et al., 2008; Andrews-Hanna, in press; see also Golland et al.,

2007; Golland et al., 2008). Moreover, default network activity is associated with many active cognitive processes that are internally focused, such as stimulus-independent thoughts or “mind-wandering” (McGuire et al., 1996; Mason et al., 2007; Christoff et al., 2009), self-reference (Gusnard et al., 2001; D’Argembeau et al., 2005) recollecting one’s past or imagining

one’s personal future (Andreasen et al., 1995; Schacter et al., 2007; Spreng et al., 2009), scene construction (Hassabis and Maguire, 2007; Hassabis et al., 2007), social cognition (Iacoboni et al., 2004; Spreng et al., 2009; Spreng and Grady, 2010; Mar, 2011; Andrews-Hanna, in press), narrative comprehension (Mar, 2011), forming associations (Bar et al., 2007), and semantic

memory (Binder et al., 2009). While many of these cognitive processes are stimulus-independent, spontaneous, and unconstrained, it is inaccurate to characterize them as “task-negative.”

The value of the “TPN vs. TNN” nomenclature has been further eroded by observations that these two putatively opposed networks can be simultaneously engaged. Specifically, the default network may be co-active, and functionally coupled, with the frontoparietal control network under certain task conditions. This evidence emerges from studies of autobiographical planning, simulated problem-solving, evaluating one’s creative work, mind-wandering, social working memory, and scene construction (Spreng et al., 2010; Summerfield et al., 2010; Gerlach et al., 2011; Ellamil et al., 2012; Meyer et al., 2012). I recently investigated interactions between purported “task-positive” and “task-negative” brain regions using two planning paradigms: visuospatial planning, as assessed by the well-established Tower of London task, and autobiographical planning, as assessed by a novel task that required participants to devise personal plans in order to meet specific goals (Spreng et al., 2010). For example, “freedom from debt” constituted one of the goals in the autobiographical planning task. Participants viewed the goal and then saw two steps they could take toward achieving that goal (“good job” and “save money”) as well as an obstacle they needed to overcome in order to achieve the goal (“have fun”). They were instructed to integrate the steps and obstacles into a cohesive personal plan that would allow them to achieve the goal. Autobiographical planning, similar to imagining personal future events (e.g., Addis et al., 2007), engaged the default network (**Figure 1B**). Visuospatial planning engaged the dorsal attention network (**Figure 1C**). Critically, both planning tasks engaged the frontoparietal control network (**Figure 1D**). Task-related functional connectivity analyses indicated that the frontoparietal control network dynamically coupled with the default network during autobiographical planning and with the dorsal attention network during visuospatial planning (**Figure 1E**). By demonstrating that the frontoparietal control network is actively engaged by two tasks that differentially rely

upon either the default or dorsal attention network, we provided novel evidence that the frontoparietal control network may flexibly gain access to information processed in either domain (for a replication and additional data with older adults, see Spreng and Schacter, in press).

Other studies have also shown co-activation of components of these networks, with tasks simultaneously driving the default and frontoparietal control networks. Gerlach et al. (2011) examined brain activity during a problem-solving task involving mental simulations. They demonstrated that, relative to a semantic processing control task, problem-solving engaged several key regions within the default network, including MPFC and PCC, as well as a region of LPFC that has been linked with executive processing. These key default and frontoparietal control structures behaved as a functional network in a multivariate functional connectivity analysis. In a recent investigation of creative idea generation and evaluation, Ellamil et al. (2012) reported that generative tasks engaged default network regions. However, during an evaluative condition, default network regions coupled with regions of the frontoparietal control network, including LPFC. Further investigations by the same group (Christoff et al., 2009; Christoff, 2012) have demonstrated that the default network is co-active and coupled with regions of the frontoparietal control network during mind-wandering. Finally, a pair of studies demonstrated co-activation, where domain specific information modulated the default network and information load modulated the frontoparietal control network: one during a social working memory task (Meyer et al., 2012), the other involved integrating imagined objects into a scene (Summerfield et al., 2010).

Mirroring earlier evidence that functionally and anatomically dissociable dorsal attention and frontoparietal control networks interact as a functional network under specific task conditions (i.e., externally directed cognition), these more recent reports provide strong evidence for interactivity among default and frontoparietal control regions during internally

directed cognition⁴. This emerging picture of dynamic interactivity among these three networks calls into question the orthodoxy of labeling functional brain networks as either TPN or TNN. These labels are more likely the byproduct of the desire for rigorously controlled experimental designs (i.e., externally directed stimuli) than meaningful descriptors of functional brain networks. However, research delineating and characterizing a taxonomy of neurocognitive networks is ongoing (e.g., Laird et al., 2011; Yeo et al., 2011). Indeed, the frontoparietal control network may be further fractionated into dissociable “salience” and “executive-control” networks (Seeley et al., 2007). Growing evidence for a complex and dynamically interacting network architecture highlight the importance of developing a stable nomenclature for functional brain networks. This will be an important consideration for future research.

Disregarding the false dichotomy of the TPN and TNN, competition between the dorsal attention and default networks may reflect competition between exogenous and endogenous loci of information processing. A critical function of cognitive control is to mediate this balance, by rapidly adapting thoughts and behaviors to changing internal states and evolving external environments. Cognitive control mechanisms promote mental flexibility by facilitating goal-directed actions and suppressing irrelevant ones. To achieve this, they must access and manipulate both exogenous and endogenous domains of information. In this way, the frontoparietal control network mediates internally and externally directed cognition by maintaining a dynamic balance between the default and attention networks (Vincent et al., 2008; Spreng et al., 2010, submitted; Smallwood et al., 2012; see also, Menon and Uddin, 2010).

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⁴Dynamic interactions between the default and frontoparietal control network have also been assessed using Granger causality during task performance (Gao and Lin, 2012) and examining low-frequency BOLD signal oscillations at rest (Deshpande et al., 2011). While compelling, these results may not be reliable (Smith et al., 2011).

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